POTENTIAL DISTRIBUTION MODELING OF *PENSTEMON OKLAHOMENSIS* (PLANTAGINACEAE)

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ABSTRACT

Penstemon oklahomensis is an endemic to the southern plains region that occurs in Oklahoma and one location in Texas. As an aid to conservation of this species, we used a species distribution model to map the possible extent of *Penstemon oklahomensis* in Oklahoma. Location data were derived from specimens in the Oklahoma Vascular Plants Database and occurrence records maintained by the Oklahoma Natural Heritage Inventory. We then modeled the potential distribution of *P. oklahomensis* with MaxEnt, a technique suitable for presence-only data. Resulting maps were used to field validate the model and determine if a gap in the southwestern portion of its range was a sampling artifact, resulting in two new first county records for the species.

RESUMEN

Penstemon oklahomensis es un endemismo del sur de la región de las llanuras que se da en Oklahoma y una localidad de Texas. Como ayuda para la conservación de esta especie, usamos un modelo de distribución de especies para mapear la posible extensión de *Penstemon oklahomensis* en Oklahoma. La posición de los datos se derivó de los especimenes existentes en la Oklahoma Vascular Plants Database y citas de ocurrencia mantenidos por el Oklahoma Natural Heritage Inventory. Luego modelamos la distribución potencial de *P. oklahomensis* con MaxEnt, una técnica apropiada para datos de solo presencia. Los mapas resultantes se usaron en el campo para validar el modelo y determinar si un hueco en la porción suroeste de su rango era un artefacto de muestreo, resultando en dos primeras citas de la especie para el condado.

INTRODUCTION

Advances in geospatial technologies and increased accessibility of species collection data have placed the mapping of species' geographical ranges at the forefront of biogeographic research and conservation planning (Guisan & Thuiller 2005; Franklin 2009; Peterson et al. 2011). Location information from natural history collections has become prevalent online in large databases (Elith et al. 2006; Newbold 2010; Peterson et al. 2011), allowing for easier mapping of a species' current and historic localities (Graham et al. 2004; Newbold 2010; Peterson et al. 2011). Likewise, efforts to collect precise location data, with the assistance of GPS, also have improved in recent years. Models of species distribution have provided insight into, generated hypotheses about a species' ecology, and aided in the location of new populations (Austin 2002; Hirzel et al. 2002; Guisan & Thuiller 2005; Franklin 2009; Lobo et al. 2010; Newbold 2010; Naimi et al. 2011).

The objective of this study was to develop a predictive range map for the distribution of *Penstemon oklahomensis* Pennell (Plantaginaceae). The genus *Penstemon* contains approximately 237 species and is one of the largest plant genera in North America (Freeman In prep; Lindgren & Wilde 2003; Nold 1999). Although *P. oklahomensis* is one of 13 species of *Penstemon* that occur in Oklahoma, it is a unique regional endemic to the southern plains region. It has been documented in 24 Oklahoma counties (Hoagland et al. 2012). In fact, all known populations were restricted to central Oklahoma until the recent discovery of a population in North Texas (Mink et al. 2010). *Penstemon oklahomensis* is a native perennial that flowers from April to mid-June and is one of only four species of *Penstemon* with a closed throat floral morphology. Of these four species, *P. oklahomensis* has the most restricted distribution (Clements et al. 1998; Pennell 1935). *Penstemon oklahomensis* most

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frequently occurs in remnant Tallgrass prairie, but has also been found in other prairie types as well as open woodlands (Hoagland et al. 2012). The Oklahoma Natural Heritage Inventory tracks *P. oklahomensis* as a state rare species (S1). At the global level, it is ranked as a G3 (either very rare and local throughout its range or found locally, even abundantly at some of its locations) and S3 (rare and local distributed within Oklahoma) (Oklahoma Natural Heritage Inventory 2012).

This project is also intended to contribute to our understanding of the ecology of *P. oklahomensis*, for which there are few published studies. A recent study of *Penstemon oklahomensis* habitat, indicated the soils where populations occur ranged from sandy loam to loam with a pH range of 5.5–7.6 and relatively low nitrogen, phosphorous, and potassium levels. The same study also found *P. oklahomensis* populations to persist in grassy roadside areas that are disturbed through various mowing regimes (Messick & Hoagland 2012).

Study Area

The study area encompasses the state of Oklahoma, although populations of *P. oklahomensis* have not been documented in western parts of the state, congeners occur in all regions. We took this approach to determine the regional extent of potential habitat. The long axis of Oklahoma has an east-west orientation that spans 6.5 degrees of longitude (from 94°30'W to 103°W) and 3.25 degrees of latitude (33°30'N to 37°N). Along this axis are two important environment gradients; elevation and precipitation. Elevation decreases from 1,516 m in the northwest, at Black Mesa, to 110 m in the southeast, where the Little River exits the state into Arkansas. Average annual precipitation also follows a northwest to southeast gradient, with the lowest values in the northwest (43 cm) and the highest in the southeast (142 cm). There is a weak south-north gradient in temperature. The length of the growing season ranges from 225-230 days along the Red River and 175 days on the border with Kansas. Average annual temperature increases roughly from 13.3°C in the northwest to 16.7°C in the southeast (Johnson & Duchon 1995).

METHODS

The successful analysis of species distribution relies upon the compilation of numerous layers of geospatial data. The primary dataset for such analyses is location data, preferably in a geographic coordinates, derived from specimen data. Location data for *P. oklahomensis* was compiled from specimen voucher data from the Oklahoma Vascular Plants Database (OVPD) (Hoagland et al. 2012), the Oklahoma Natural Heritage Inventory (ONHI) (Oklahoma Natural Heritage Inventory 2012), and other sources (Freeman 1981). As noted earlier, a population of *P. oklahomensis* has been reported from northeastern Texas, which is 51.5 km from the nearest Oklahoma population (Mink et al. 2010), and was excluded from this analysis due to a lack of detailed information on the population in question and access to geospatial data for Texas. We recognize the importance of this population, however, and encourage the exploration of intervening areas between the Texas and Oklahoma populations

Once extracted, location data were compiled into a geodatabase and edited to remove duplicate records. Duplicate records were found primarily in the OVPD and are a byproduct of specimen exchanges between in-state institutions. Duplicate records also existed between the OVPD and the ONHI database. Next, geographic precision of the records was assessed. Geographical coordinates were not provided on the majority of herbarium vouchers predating 2000, but either driving directions and/or land survey references (e.g., township, range, and section) were recorded. Thus it was necessary to manually assign geographical coordinates. Specimens that listed only the county or equally vague geographic reference (e.g., Indian Territory) were excluded from analysis. The resulting dataset for analysis consisted of 142 location points (Fig. 1).

When mapping species distributions, it is important to examine both the extent of occurrence (EOO) and area of occupancy (AOO). The EOO represents the entire area in which a species has been found, including gaps between populations, and is bounded by the outermost occurrences of a species. The gaps between populations may simply represent inadequate sampling effort or are possibly areas of unsuitable habitat. The EOO for a species can be mapped using the convex hull operation. The resulting map is a more accurate depiction of a species distribution than one created using rectangles or circles encompassing all known locations of a spe-

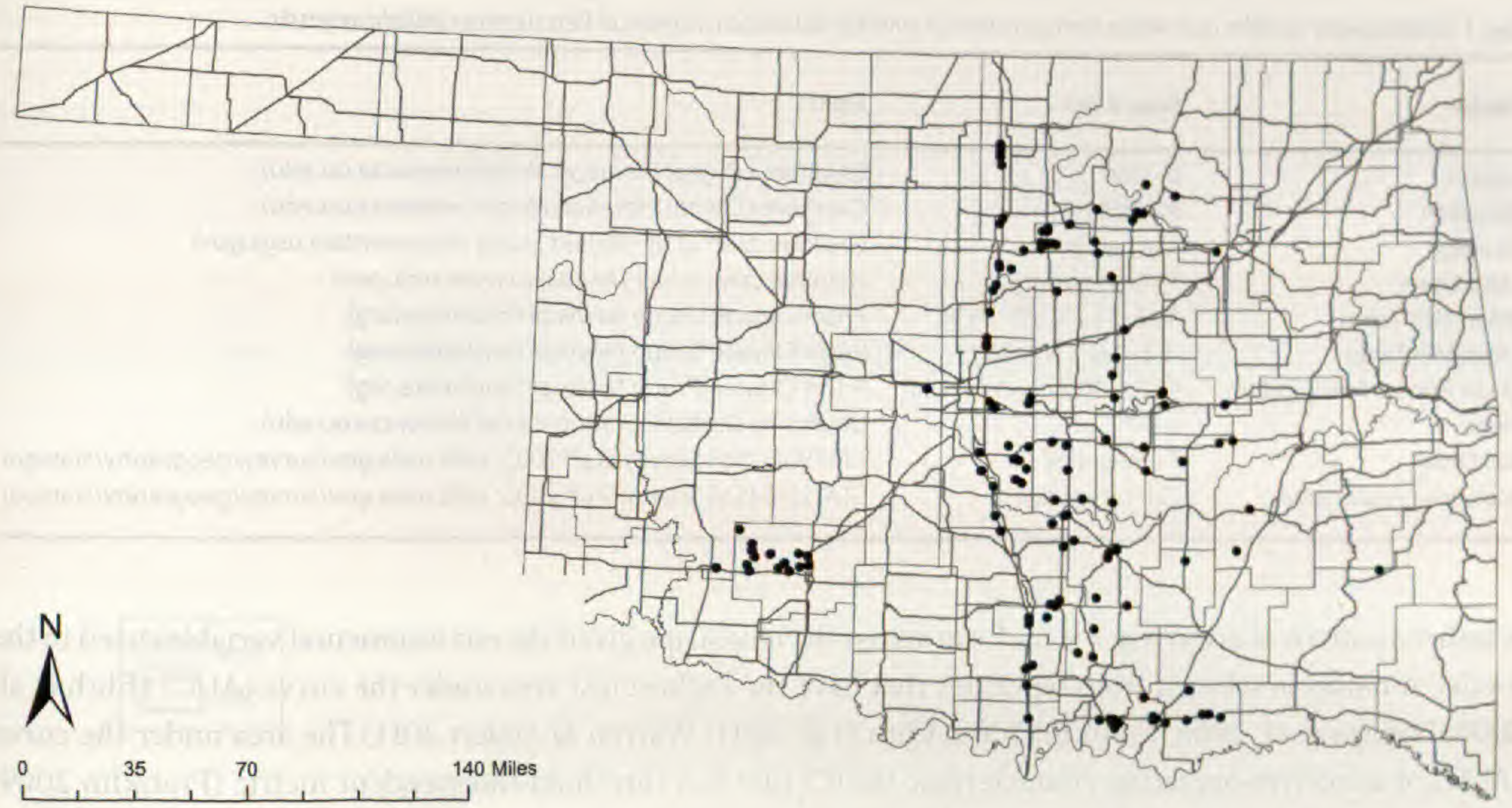

Fig. 1. Point distribution map of *Penstemon oklahomensis* in Oklahoma, includes interstate and state highways before modeling.

cies (Podani 2009). The AOO is the area where the target species is actually found and is either equal to or smaller than the EOO. The AOO does not include gaps between populations. Removing gaps or discontinuities in an EOO results in the AOO for a species (Gaston & Fuller 2009).

The EOO map of *P. oklahomensis* was generated using the Convex Hull module of ArcGIS 10 using the species occurrence data layer. Upon inspection, the resulting map exhibited a significant gap in the species distribution between central and southwestern Oklahoma. Thus, we repeated the convex hull operation so that the southwestern Oklahoma collection points (n=15) were aggregated into a polygon separate from a larger central Oklahoma area polygon.

Maximum entropy (MaxEnt), the method most frequently used in species distribution modeling, was chosen for modeling the distribution of *P. oklahomensis*. (Franklin 2009; Naimi et al. 2011). MaxEnt was designed specifically for use with presence-only data, such as the *P. oklahomensis* dataset, and can analyze small sample sizes (< 100 samples) and overcome sampling bias (Franklin 2009).

MaxEnt analyzes species occurrence data in conjunction with a suite of environmental data to calculate an index of relative suitability for a species (Graham et al. 2008; Anderson & Gonzalez 2011; Elith et al. 2011). Environmental factors are independent variables and are referred to as covariate or predictor variables. The environmental variables used in this study were elevation, slope, aspect, land cover type, soil order, soil series, geology, mean minimum annual temperature, mean maximum annual temperature, and mean annual precipitation (Table 1). Slope and aspect were derived from a 30 m DEM using ArcGIS Spatial Analyst Toolbox and then clipped to the political boundaries of Oklahoma. All of the remaining environmental variables were acquired as vector data and were converted to raster format to match the extent and scale of the DEM.

MaxEnt attempts to derive a log-linear model that is dependent on the presence points and a set of selected randomly from the environmental data layers, referred to as background points, to estimate the probability of an occurrence or population in a locality. Should an actual species presence point be selected as a background point, then the environmental features are rescaled on a scale of 0–1, and an error boundary for the point is calculated. The error bounds are calculated from the environmental features rather than the presence points because the presence points are often biased (Elith et al. 2011).

Model evaluation

The output of MaxEnt is a probability of species occurrence based on the concept of maximum entropy or

Table 1. Environmental variables used within MaxEnt models for potential distribution mapping of *Penstemon oklahomensis*.

Variable	Range & Unit	Source
Aspect	0–359°	Oklahoma Digital Elevation Model (www.csa.ou.edu)
Elevation	87–806 m	Oklahoma Digital Elevation Model (www.csa.ou.edu)
Geology	156 categories	Geologic Map of the United States (www.mrdata.usgs.gov)
Land Cover	15 categories	National Land Cover Database (www.mrlc.gov)
Mean Max Temp	30.5–37.2°C (87–99°F)	Prism Climate Group (www.prismclimate.org)
Mean Min Temp	-8.3–0.6°C (17–33°F)	Prism Climate Group (www.prismclimate.org)
Mean Annual Precipitation	43.2–180.3 cm (17–71 in)	Prism Climate Group (www.prismclimate.org)
Slope	0–57°	Oklahoma Digital Elevation Model (www.csa.ou.edu)
Soil Order	7 categories	STATSGO (Soil Survey Staff 2005; soils.usda.gov/survey/geography/statsgo)
Soil Series Association	228 categories	STATSGO (Soil Survey Staff 2005; soils.usda.gov/survey/geography/statsgo)

whether a pattern of occurrence is uniform across the landscape given the environmental variables used in the model. A model is selected from replicates that have the highest test area under the curve (AUC) (Elith et al. 2006; Phillips et al. 2006; Franklin 2009; Elith et al. 2011; Warren & Seifert 2011).The area under the curve (AUC) of a receiver-operating characteristic (ROC) plot is a threshold-independent metric (Franklin 2009; Jimenez-Valverde 2012). A ROC plot graphs "the false-positive error rate on the x-axis (1 - Specificity) versus the true positive rate on the y-axis (Sensitivity) based on each possible value of threshold probability" (Franklin 2009). The AUC is calculated from the resulting curve and can range from 0.5 to 1.0. The value 0.5 represents random predictions while values above 0.5 represent "performance better than random" (Franklin 2009; Jimenez-Valverde 2012). An AUC value between 0.5 and 0.7 indicates low or poor performance, between 0.7 and 0.9 indicates moderate performance, and values greater than 0.9 indicate high performance (Swets 1988; Franklin 2009).

We used MaxEnt version 3.3.3e modeling software (www.cs.princeton.edu/~schapire/maxent) to model the potential distribution of *P. oklahomensis*. The analysis was run with 0%, 10%, 20%, 30%, 40%, and 50% of the *P. oklahomensis* point locations withheld for testing the model. Collectively these model runs were called Model Set A. For each percentage category for which points were withheld, 15 replicates were generated. Response curves, jackknife of variable importance, and maps of predicted distributions were also generated. The jackknife of variable importance identifies the individual variable(s) that were most important in predicting the species' distribution (Elith et al. 2011). In order to evaluate the potential outlier affect of the *P. oklahomensis* occurrence in eastern Oklahoma, the analysis was conducted a second time and the resulting models were referred to as Model Set B.

MaxEnt created grids for the average, minimum, maximum, median, and standard deviation of the predictions for each percentage category withheld run based on the test AUC value. The average prediction grids were converted to raster files and the resulting prediction AUC values were then compared. Based on the prediction maps, the gap in the distribution between the southwestern populations and the central populations was surveyed for *P. oklahomensis* populations. This area included three counties; Grady County, Stephens County, and Jefferson County. If a *P. oklahomensis* population was discovered, voucher specimen was collected and deposited at the Robert Bebb Herbarium (OKL) at the University of Oklahoma, Norman, OK.

RESULTS AND DISCUSSION

The county-level map of the 142 *Penstemon oklahomensis* (Fig. 1) location points revealed that the majority of collection points were both in central Oklahoma and clustered near interstate or state highways. To verify this pattern, we calculated Moran's I (I), which proved a significant pattern ($I = 0.371$, z score $= 3.385$, $p = 0.001$). Also, the AOO for this species was much smaller in area than the EOO and as noted earlier, there were two noteworthy gaps in the EOO; the first in the southeast and a second in the southwest (Fig. 2). Since the gap in the southwest was more pronounced geographically and was represented by a greater number of occurrences

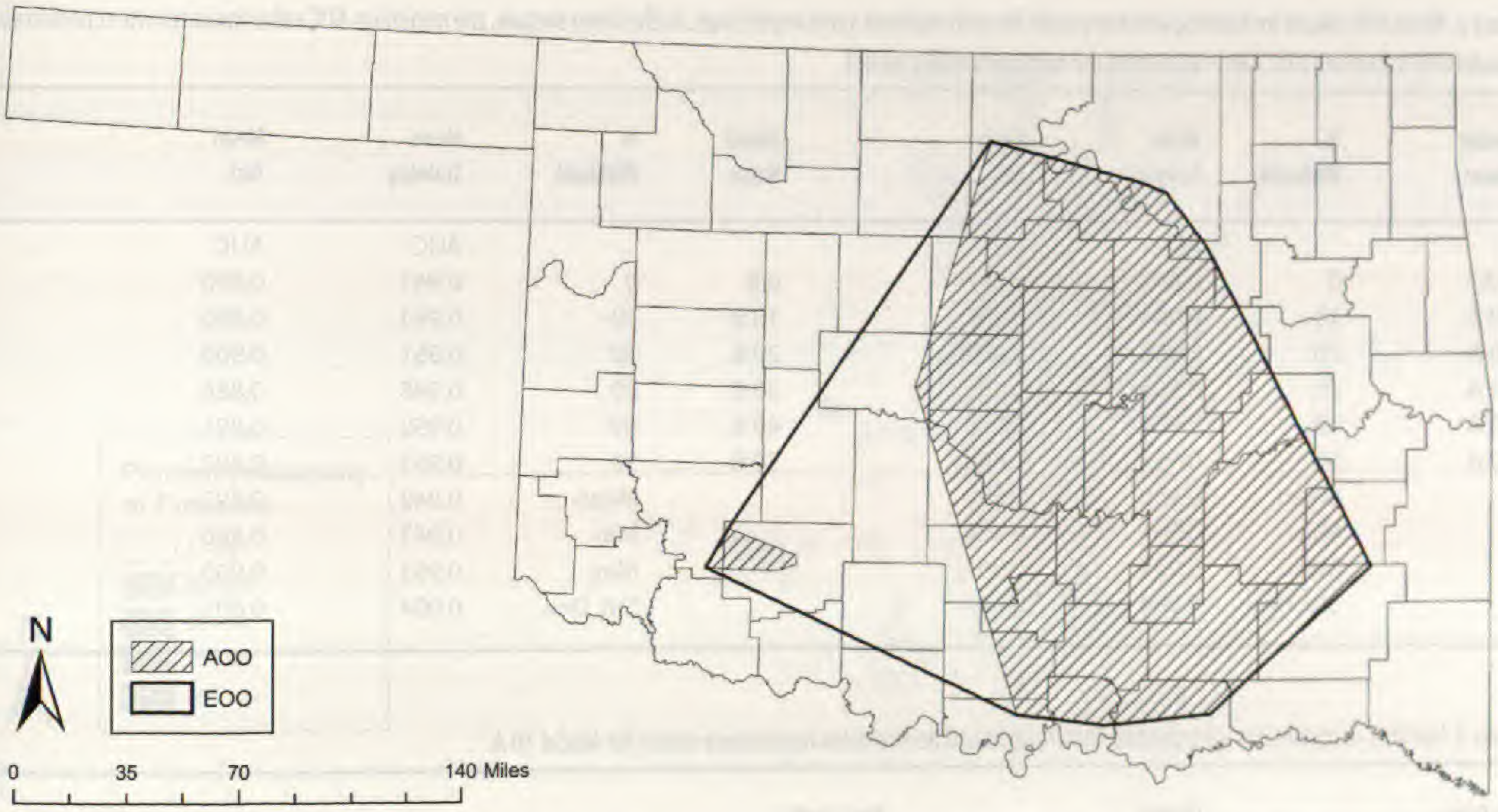

FIG. 2. Extent of occurrence (EOO) and area of occupancy (AOO) for *Penstemon oklahomensis* within Oklahoma before modeling.

(n=15) than the southeast (n=1), it became the focus of our analysis and groundtruthing. Our goal was to ascertain whether this was a true gap in distribution or a sampling artifact.

The training and test AUC values for both model sets are listed in Table 2. Model 40 A had the highest training AUC (0.954) while Model 10 A had the lowest training AUC (0.944). For the test data, Model 10 A had the highest AUC (0.907) and Model 50 A had the lowest AUC (0.889). From the test data used in Model 10 A, the jackknife of the environmental variables showed geology (25.6% contribution) and soil series association (20.6% contribution) to be the most important (Table 3). Model 50 B had the highest training AUC (0.953) and Model 0 B had the lowest training AUC (0.943). For the test data, Model 20 B had the highest AUC (0.900) and Model 30 B had the lowest AUC (0.886). The jackknife of environmental variables from the test data used in Model 20 B also showed geology (27.7% contribution) and soil series association (22.2% contribution) to be the most important (Table 4). Model 20 B (Fig. 3) was selected as the best predictive map for the potential distribution of *P. oklahomensis* within Oklahoma because of its AUC value even though the value is the cut-off value (0.900) between moderate and high performance according to Swets' scale (1988).

Groundtruthing

MaxEnt predicted greater than 25% probability of occurrence of *P. oklahomensis* populations in extreme northern Grady County and another in southern Grady County, a location within the southwestern distribution gap. The two predicted northern locations were surveyed, but one proved to be a wheat field and the other a grazed pasture. A new population (Fig. 4) of *P. oklahomensis* was located, however, at the southern location where the model predicted 25%–49% probability of occurrence. Another locality within the portion of Stephens County in the gap, with a greater than 25% probability of an occurrence was surveyed, but no populations were found. A predicted location in northern Stephens County, with less than a 25% probability of occurrence, did produce a new population (Fig. 4). Additional surveys of counties in the southwestern gap did not yield new populations of *P. oklahomensis*.

The point locations of the new populations were added to the overall point distribution map and the probability values extracted from the model. The Grady County population probability value was 0.21 and the value for the Stephens County population was 0.03. The two new location points were added to the same dataset used to produce Model Set B, and MaxEnt run again with the same settings to produce Model Set C. The AUC

TABLE 2. Mean AUC values for training and test points for each replicate set of models run. In the lower section, the minimum AUC value indicates worst performing model and maximum AUC value represents the best performing model.

Model Name	% Withheld	Mean Training	Mean Test	Model Name	% Withheld	Mean Training	Mean Test
		AUC	AUC			AUC	AUC
0 A	0	0.947	0.897	0 B	0	0.943	0.890
10 A	10	0.944	0.907	10 B	10	0.944	0.896
20 A	20	0.950	0.906	20 B	20	0.951	0.900
30 A	30	0.952	0.895	30 B	30	0.948	0.886
40 A	40	0.954	0.898	40 B	40	0.950	0.891
50 A	50	0.952	0.889	50 B	50	0.953	0.892
	Mean	0.950	0.899		Mean	0.948	0.892
	Min	0.944	0.889		Min	0.943	0.886
	Max	0.954	0.907		Max	0.953	0.900
	Std. Dev.	0.004	0.007		Std. Dev.	0.004	0.005

TABLE 3. Variable contributions with percent contribution and permutation importance values for Model 10 A.

Variable	Percent Contribution	Permutation Importance
Geology	25.6	17.7
Soil Series	20.6	13.9
Precipitation	19.7	7.6
Land Cover	13.2	8.6
Soil Order	5.4	6.5
Slope	4.9	5.3
Min Temp	4.8	15.9
Elevation	4.8	20.6
Aspect	0.5	0.8
Max Temp	0.4	3.0

TABLE 4. Variable contributions with percent contribution and permutation importance values for Model 20 B.

Variable	Percent Contribution	Permutation Importance
Geology	27.7	14.7
Soil Series	22.2	17.7
Land Cover	13.0	9.8
Precipitation	10.7	3.2
Soil Order	9.5	7.7
Elevation	5.6	13.4
Min Temp	5.3	20.0
Slope	5.1	10.2
Max Temp	0.5	2.8
Aspect	0.5	0.7

values of Model Set C are listed in Table 5. Adding the new location points to the dataset lowered the AUC values of all models into the moderate performance range, contrary to expectation.

CONCLUSION

Our objective was to glean a better understanding of factors controlling the distribution of *Penstemon oklahomensis* across its geographic range. Data for this effort was collected from Freeman (1981), OVPD (Hoagland et

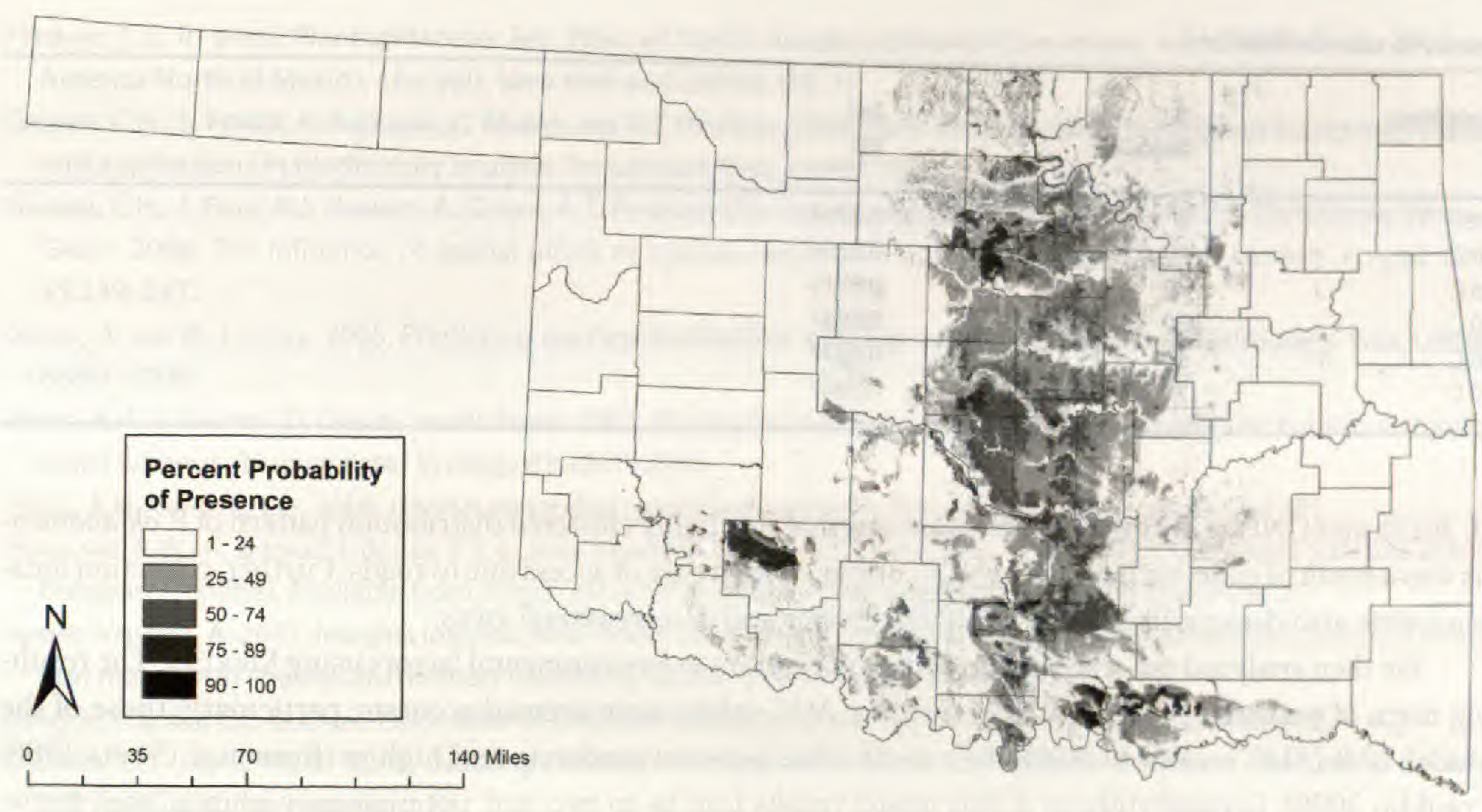

Fig. 3. Prediction map for *Penstemon oklahomensis* potential distribution within Oklahoma; Model 20 B.

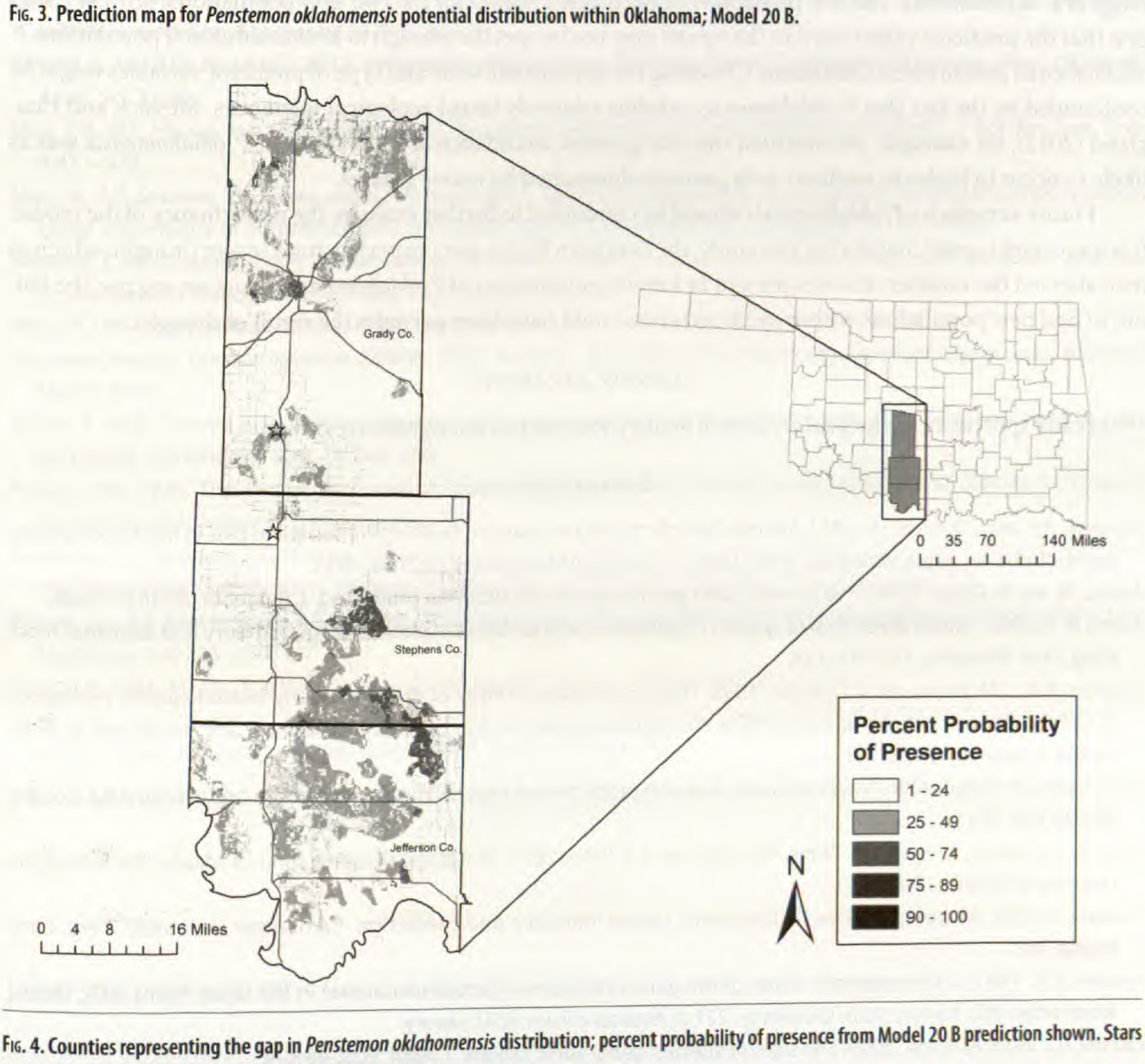

Fig. 4. Counties representing the gap in *Penstemon oklahomensis* distribution; percent probability of presence from Model 20 B prediction shown. Stars indicate location of newly located populations.

TABLE 5. AUC values for Model Set C.

Model Name	% Withheld	Test AUC
0 C	0	0.8944
10 C	10	0.8859
20 C	20	0.8819
30 C	30	0.8837
40 C	40	0.8877
50 C	50	0.8851

al. 2012), and ONHI. Our initial observation was that the highly clustered distribution pattern of *P. oklahomensis* was a result of collector bias, which was correlated with ease of access due to roads. Further, collection locations were also clustered near cities with universities and in recreational areas.

We then analyzed the relationship of the distribution to environmental factors using MaxEnt. The resulting maps of potential probability of occurrence AUC values were deemed accurate, particularly those of the Model 20 B (AUC = value of 0.90), the cut-off value between moderate and high performance (Swets 1988; Franklin 2009). Groundtruthing of this model results lead us to two new populations within a "gap" in the range of *P. oklahomensis*. The low probability of occurrence values for the two new populations, however, suggest that the predictor values used in the model may not be specific enough to locate additional populations *P. oklahomensis* in southwest Oklahoma. Choosing the appropriate scale and type of predictor variables might be confounded by the fact that *P. oklahomensis* exhibits relatively broad ecological tolerances. Messick and Hoagland (2012), for example, documented that the greatest abundance of individuals of *P. oklahomensis* was as likely to occur in highway medians as in pastures dominated by native grasses.

Future surveys for *P. oklahomensis* should be conducted to further evaluate the performance of the model. It is important to note that during this study, the Southern Plains were experiencing a severe drought, which in turn affected the number of stems present in known populations of *P. oklahomensis*. Thus we suggest the failure to find new populations within predicted areas could have been partially the result of drought.

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